Independent coding of object motion and position revealed by distinct contingent aftereffects

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Abstract

Despite several findings of perceptual asynchronies between object features, it remains unclear whether independent neuronal populations necessarily code these perceptually unbound properties. To examine this, we investigated the binding between an object's spatial frequency and its rotational motion using contingent motion aftereffects (MAE). Subjects adapted to an oscillating grating whose direction of rotation was paired with a high or low spatial frequency pattern. In separate adaptation conditions, we varied the moment when the spatial frequency change occurred relative to the direction reversal. After adapting to one stimulus, subjects made judgments of either the perceived MAE (rotational movement) or the position shift (instantaneous phase rotation) that accompanied the MAE. To null the spatial frequency-contingent MAE, motion reversals had to physically lag changes in spatial frequency during adaptation. To null the position shift that accompanied the MAE, however, no temporal lag between the attributes was required. This demonstrates that perceived motion and position can be perceptually misbound. Indeed, in certain conditions, subjects perceived the test pattern to drift in one direction while its position appeared shifted in the opposite direction. The dissociation between perceived motion and position of the same test pattern, following identical adaptation, demonstrates that distinguishable neural populations code for these object properties.
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1. Introduction

The visual system efficiently decomposes and processes images in a distributed and parallel manner (Livingstone & Hubel, 1988; Livingstone & Hubel, 1987). Because information processed in distinct pathways must be recombined into common representations, the visual system may face a binding problem in order to perceive coherent objects and scenes (Humphreys, 2003; Treisman, 1993, 1996; Wolfe & Cave, 1999). Alternatively, the awareness of different sorts of visual information might be determined in separable modules (Bartels & Zeki, 1998;

Fodor, 1983; Zeki, 2001; Zeki & Bartels, 1998), which could either postpone or obviate the need for a central executive to "bind" information. There is neurological evidence in favor of modularity (from a variety of agnosias (Humphreys, 2003; Zeki & Bartels, 1999; Zihl, von Cramon, & Mai, 1983), although see (Lennie, 1998), for counterarguments). There is also psychophysical evidence for modular processing of visual features; in addition to evidence from visual search paradigms (Treisman, 1998), many recent studies have reported distinct perceptual time-courses for different visual attributes, such as motion and color (Moutoussis & Zeki, 1997), though, as with the neurological case studies, the psychophysical evidence for differential perceptual latencies remains hotly debated (Nishida & Johnston, 2002; Ogmen, Patel, Bedell, & Camuz, 2004; van de Grind, 2002). What is needed is

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definitive evidence that there are separable populations of neurons that both code and independently give rise to the perception of different visual attributes.

1.1. Differential temporal profiles for stimulus attributes

Several groups have used a number of paradigms to reveal what appear to be differential perceptual latencies for different stimulus attributes (Arnold, Clifford, & Wenderoth, 2001; Arnold, Durant, & Johnston, 2003; Bedell, Chung, Ogmen, & Patel, 2003; Clifford, Arnold, & Pearson, 2003; Hess & Holliday, 1992; Libet, 1993; Moutoussis & Zeki, 1997; Ogmen et al., 2004; Purushothaman, Patel, Bedell, & Ogmen, 1998; van de Grind, 2002; Whitney, 2002; Whitney & Murakami, 1998). One of the most direct but contested of these paradigms is the color-motion asynchrony (Moutoussis & Zeki, 1997). In this illusion, a change in an object's direction of motion is perceived to lag behind the object's change in color, even when these changes are physically synchronous. These results suggest that the time needed to perceive color may be more rapid than that for motion reversals, although this is intensely debated (Arnold et al., 2001, 2003; Bedell et al., 2003; Clifford et al., 2003; Johnston & Nishida, 2001; Moutoussis & Zeki, 1997; Nishida & Johnston, 2002).

Arnold and colleagues (Arnold et al., 2001) provided strong evidence for the notion that different stimulus features have different perceptual time-courses by measuring a color-contingent MAE across a range of phase combinations of color and motion changes. The color-contingent MAE is an illusion in which an object's direction of motion is paired with a specific color in an oscillating stimulus (Favreau, Emerson, & Corballis, 1972; Hepler, 1968). Following adaptation, the direction of the MAE is contingent on the color of the test grating (Favreau et al., 1972). In addition to color, the MAE can be made to be dependent on other feature dimensions (Mayhew, 1973a, 1973b; Mayhew & Anstis, 1972) and can be determined by the eye(s) exposed to the motion (Anstis & Duncan, 1983) or the direction of gaze (Mayhew, 1973a; Nishida, Motoyoshi, Andersen, & Shimojo, 2003). Surprisingly, Arnold and colleagues (Arnold et al., 2001) found a contingent MAE even when subjects adapted to a stimulus whose direction of motion was paired with equal durations of each color (perfectly asynchronous pairings of direction and color should produce no contingent aftereffects). The implication of these results is that the adapting neurons must receive incoming visual information at different rates to optimally adapt. The color change had to occur ~80 ms after the direction reversal to null any contingent MAE.

Although the color-contingent MAE data suggests different processing latencies for color and motion, this conclusion has recently been questioned (Bedell et al., 2003; Clifford et al., 2003; Johnston & Nishida, 2001; Nishida & Johnston, 2002). The differential latency hypothesis, in its strongest and simplest form, argues that color and direction signals arrive at the adapting neural population at different moments. A modified account, however, suggests that it may not be the moment at which signals arrive at the adapting units that matters, but rather the temporal profile of activity produced by color and motion (Arnold & Clifford, 2002; Bedell et al., 2003; Clifford et al., 2003). If color and direction changes each produce a characteristic but different pattern of activity over time, aligning these two different profiles might produce what appear to be differential latencies but are more appropriately described as different temporal response patterns. Different levels of adaptation over time (Clifford et al., 2003), differential inhibition over time (Arnold & Clifford, 2002; Bedell et al., 2003; Clifford et al., 2003), or misbound "time markers" (Nishida & Johnston, 2002) in the systems that process color and motion could each explain how distinct temporal response patterns might arise. Given opponent motion processes, for example, there may be more inhibition when a moving pattern reverses direction, which could explain why the color motion asynchrony is strongest for motion reversals compared to other kinds of direction changes (Bedell et al., 2003; Clifford et al., 2003).

1.2. Dissociating stimulus dimensions: Motion versus position

Studies of object motion and position also provide evidence that the visual system may process information in distinct modules. The perceived position of an object, for example, can appear displaced in one direction without producing the perception of motion, suggesting that the object's motion may be coded independently from its position (Sheth, Nijhawan, & Shimojo, 2000; Watanabe, Nijhawan, & Shimojo, 2002; Whitney, 2002). Unfortunately, this is a one-way dissociation and therefore relatively weak evidence; rather than being due to separable modules for position and motion perception, the dissociation could arise after the stage at which motion and position are actually coded. Moreover, most models of motion perception and related psychophysical data demonstrate that the structure or texture of a moving pattern is coded along with the perceived direction of the pattern's movement (Burr & Ross, 2002; Geisler, 1999; Nishida, 2004). Therefore, there is only weak evidence that the motion and position of an object are processed in independent pathways and that these can be fully dissociated. If we could provide further evidence for this dissociation, however, we would be able to demonstrate that at least some dimensions of a single object are independently processed in separate modules.

1.3. Linking stimulus dissociations and differential temporal profiles

The present study seeks to determine whether the perceived motion and position of an object can be fully dissociated in space and in time. We used a spatial frequency (texture) contingent MAE to measure the MAE as well as

the position shift that accompanies the MAE (McGraw, Whitaker, Skillen, & Chung, 2002; Nishida & Johnston, 1999; Snowden, 1998; Whitaker, McGraw, & Pearson, 1999; Whitney & Cavanagh, 2003). Following adaptation to a stimulus with systematic phase pairings of spatial frequency and motion (Fig. 1; see Section 2), we measured both the MAE and the perceived position (i.e., instantaneous phase) of the test stimulus (Fig. 1b and c). Our goal was to measure the time-course of contingent adaptation for judgments of motion and position, and, further, to determine whether an object can appear to move in one direction while its position is perceived to shift in the opposite direction. Establishing both temporal as well as spatial dissociations between the percept of two dimensions (motion and position) within a single object would be strong evidence that stimulus attributes are coded independently.

2. Methods

2.1. General methods

Four experienced psychophysical subjects with normal or corrected-to-normal visual acuity participated in all experiments. Stimuli were presented on a high-resolution CRT monitor (Samsung SyncMaster 997DF, 800×600 pixels, 100 Hz refresh) controlled by an Apple G4 Power Macintosh running OS9. Subjects were seated in a dark room and immobilized with a chinrest placed 35 cm from the screen. Subjects used the computer keyboard to make their responses.

Throughout the experiments, subjects maintained fixation on a central white (71.5 cd/m^2) bull's-eye (1.5 deg diameter) against a black background (0.44 cd/m^2) presented at eye level. Two circular adaptation gratings (13.5 deg diameter) were centred 8 deg to either side of fixation, rotating in the same direction (4.35 Hz; Fig. 1). The nearest separation between the two gratings was 2.5 deg. These radial gratings oscillated clockwise and anticlockwise at 1 Hz (oscillation frequency) and changed from low to high spatial frequency with the same temporal frequency (1 Hz). Low spatial frequency (four cycles per rotation) and high spatial frequency (fourteen cycles per rotation) patterns were composed of sine wave luminance modulations (74% Michelson contrast).

During adaptation, the spatial frequency and motion changes could be presented synchronously (0 or 180 deg phase offset), or with a relative phase delay (Fig. 1d). For example, at 0 deg phase the low spatial frequency was paired synchronously with clockwise motion throughout the adaptation. At 72 deg phase offset, the spatial frequency change was delayed 200 ms relative to the change in motion direction. Because the adaptation grating reversed direction every 500 ms (one full cycle equals 1 s), each 100 ms incremental delay between spatial frequency and motion was equivalent to a 36 deg temporal phase shift. A 90 deg phase offset meant that equal durations of each direction of motion were paired with equivalent durations of each spatial frequency. Phase offsets between 180 and 360 deg were mirror reversed versions of the 0–180 deg phase offset conditions (e.g., the relationship between spatial frequency and direction of motion was mirror reversed such that at 180 deg the clockwise motion period was synchronous with the high spatial frequency pattern).

2.2. Experiment 1: Spatial frequency-contingent MAE

Modelled closely after the methods of Arnold and colleagues (Arnold et al., 2001), the first experiment measured the spatial frequency-contingent MAE. During an initial 62.5 s adaptation period, the motion reversals and spatial frequency changes occurred at one phase relationship (e.g., 72 deg phase shift). After this adaptation period (100 ms ISI), the radial gratings were again presented in a test period (500 ms). These test gratings

were slowly rotated at one of seven speeds ranging from ±0.16 Hz centred around zero (stationary); the two test gratings (Fig. 1b) always rotated in the same direction. The test gratings were identical in size and location to the adaptation gratings, and were either a low or high spatial frequency
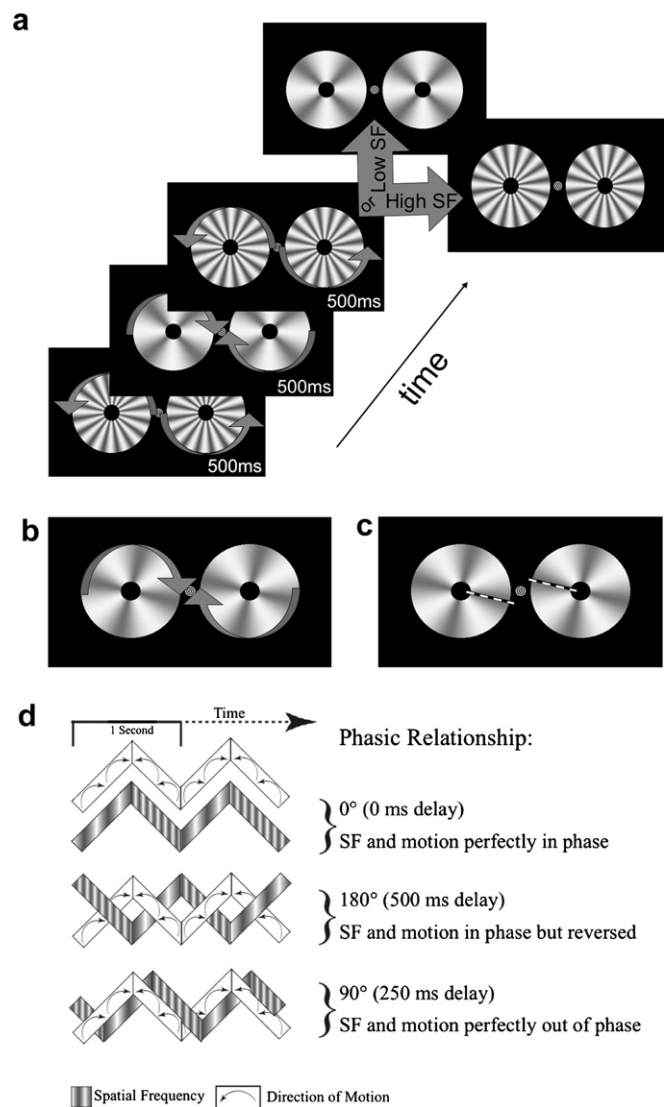

Fig. 1. Experimental stimulus and procedure. (a) Subjects adapted to an oscillating radial grating that alternated between high and low spatial frequency. The timing of the direction reversals relative to the spatial frequency changes was manipulated in separate sessions. In this example, the direction and spatial frequency changes of the grating are phase-locked (0 deg phase difference). During the test period (top 2 tiled panels of (a)), a high or low spatial frequency test grating could be presented. Following adaptation to phase-locked direction and spatial frequency information, contingent aftereffects can result. (b,c) In separate sessions, but after identical adaptation, the spatial frequency-contingent motion aftereffect (MAE) and position shift were measured. The MAE was measured as the physical motion required to null any perceived motion (b). The position shift that follows motion adaptation was measured as the physical phase shift required to null the apparent misalignment between the nearest spokes of the static test grating (c). The black and white dashed line in (c) and directional arrows in (b) were not visible in the experiment. (d) In separate sessions, the timing (phase offset) of the motion reversals relative to the spatial frequency changes during adaptation was manipulated. The example from (a) is shown in the top panel, in which clockwise motion was synchronously paired with low spatial frequency. Phase offsets of 180 and 90 deg are shown in the panels below.

pattern (to produce a contingent MAE). The initial phase of each test grating was randomized on each trial. Following this initial adaptation and test period, 3 s top-up and 0.5 s test periods were interleaved through the remainder of the session. One experimental session consisted of 10 trials for each of 7 rotation speeds and 2 test grating spatial frequency patterns (low or high) for a total of 140 trials per session. Each subject participated in at least 3 sessions for each of 4 phase offsets (72 and 108 deg and the equivalent mirror reversed conditions 252 and 288 deg), for a total of at least 1680 trials. Different adaptation conditions (different phase offsets) were tested in sessions separated by at least one day. One subject (PB) was tested across the entire range of 10 possible phase offsets (increments of 36 deg) between spatial frequency and motion changes (8400 trials). The reason for testing primarily the 72, 108, 252, and 288 deg phase offset conditions is because these conditions are centred around the conditions in which the motion and spatial frequency changes are perfectly out of phase (i.e., at 90 and 270 deg phase offset, the contingent adaptation is completely asynchronous and there should be no contingent aftereffect).

Using a method of constant stimuli task, subjects made a two-alternative forced choice (2AFC) judgment of which directions the test gratings rotated. A logistic function, $f(x) = [1/(1 + \exp[a(x + b)])]$, was fit to the data, revealing the cumulative probability that subjects perceived motion in the direction of adaptation; parameter (a) is the slope of the psychometric function, and parameter (b) estimates the point of subjective equality (PSE), which reveals the physical rotation of the test grating that made the grating appear stationary. To null a perceived MAE on the stationary test gratings would require rotation in the direction of adaptation. In each condition, there were two psychometric functions—for low and high spatial frequency test patterns. The magnitude of the contingent aftereffect was calculated as the difference in the PSEs for high minus low spatial frequency patterns; no difference indicates a lack of contingent aftereffect. For each subject, a PSE was calculated for each of the six sessions in each condition, and PSEs were averaged across sessions to give a single PSE for each phase offset.

2.3. Experiment 2: Spatial frequency-contingent position shift

In a separate experiment, but using the same adaptation and test stimuli as above, subjects judged the perceived position (spatial phase) of the radial grating (rather than judging the direction of motion). During the test periods, either a low or high spatial frequency radial grating was presented for 200 ms, which reduced the influence of any perceived motion. The spatial phase of the test grating could be misaligned by one of seven values ranging within ±11 deg of phase (Fig. 1c). In a 2AFC task, subjects judged the direction of misalignment between the phases of the radial gratings (a vernier alignment between the central spokes). The PSE on the psychometric function reveals the physical misalignment between the radial grating that created an apparent alignment. As with the MAE judgment, each session consisted of 10 trials collected for 7 alignments and 2 test patterns (low or high). Subjects completed at least 3 sessions of the 72, 108, 252, and 288 deg phase offset conditions, for a grand total of at least 1680 trials. Subjects participated in both the position shift and MAE experiments (two separate tasks) in interleaved blocks to reduce order or experience-dependent effects. Data were analyzed as they were for the contingent MAE. The main effects and interactions between judgment type and phase offset were computed with ranked ANOVAs (Yandell, 1997) and Mann–Whitney *U* tests, as the units are different for the two measures.

2.4. Experiment 3: Color-contingent MAE and position shift

To replicate the study of Arnold et al. (2001), we measured the color-contingent MAE in an additional experiment. We also measured the color-contingent position shift using the same stimuli. The methods and stimuli were identical to those above, with the exception that high and low spatial frequency defined patterns were replaced with red and green gratings (eight cycles per rotation, same contrast, size, location, and procedures). The minimum motion technique was used to establish the psychophysical equiluminance between the red and green gratings (Anstis & Cavanagh, 1983; Arnold et al., 2001; Seiffert & Cavanagh, 1999). To do this, red and green gratings drifting in opposite directions were superimposed; the red grating's contrast was fixed at 70%, and the relative contrast of the green grating was manipulated in a 2AFC method of constant stimuli task. The PSE measured the relative contrast of the green grating required to null the perceived motion of the stimulus. The relative red and green contrasts required to null the perceived motion were measured for each subject. The equiluminant color-contingent MAE and position shift were then measured, using the methods described above for spatial frequency defined patterns.

3. Results

Fig. 2a and b shows the perceived spatial frequency-contingent MAE, for two individual subjects, as a function of the phase relationship between the spatial frequency and the direction (Fig. 1d, see Section 2). The data in Fig. 2b are collapsed across mirror symmetric phase conditions to facilitate interpretability. For example, 72 and 252 deg are mirror symmetrical conditions: in both conditions, the change in spatial frequency in the adapting stimulus physically lagged behind the direction reversal by 200 ms (only the initial direction of motion was different at 72 and 252 deg). The zero crossing on the graph in Fig. 2b indicates the relationship between attribute changes that elicits no contingent aftereffect. For instance, if no asynchronies exist between spatial frequency and motion, then motion direction reversals that are 90 deg out of phase with spatial frequency changes should produce no contingent aftereffect (i.e., one spatial frequency pattern would rotate both clockwise and counterclockwise for equal durations). Fig. 2b shows that in both conditions straddling the critical 90 deg phase pairing (vertical dashed line), there was a spatial frequency-contingent MAE.

In the second experiment, we measured the perceived position shift of test gratings after adaptation the same stimuli used in the first experiment to measure the spatial frequency-contingent MAE (results for one representative subject shown in Fig. 2c and d). Position judgments followed a time-course similar to that expected if there were synchronous processing of spatial frequency and motion changes. That is, the subject perceived little or no contingent position shift after adapting to the same oscillating stimulus that did produce a contingent MAE. This is revealed by the zero crossing in Fig. 2d, which is very close to the vertical dashed line, where the spatial frequency and motion direction are 90 deg out of phase.

Fig. 3 shows a comparison between the spatial frequency-contingent motion and position aftereffects for all subjects in the critical adaptation conditions (those near 90 deg phase offset). Despite the identical adaptation conditions in both experiments, the time-course and direction of the contingent *motion* aftereffect was different than that of the contingent *position* aftereffect. For example, at 72 deg phase offset, the MAE was above zero ($t_{(3)} = -4.92$, $P = 0.008$), while the contingent position shift was below zero ($t_{(3)} = 2.7$, $P = 0.035$). That is, the perceived MAE was in a direction opposite that of the contingent position shift, despite the same adaptation. A closer examination of the
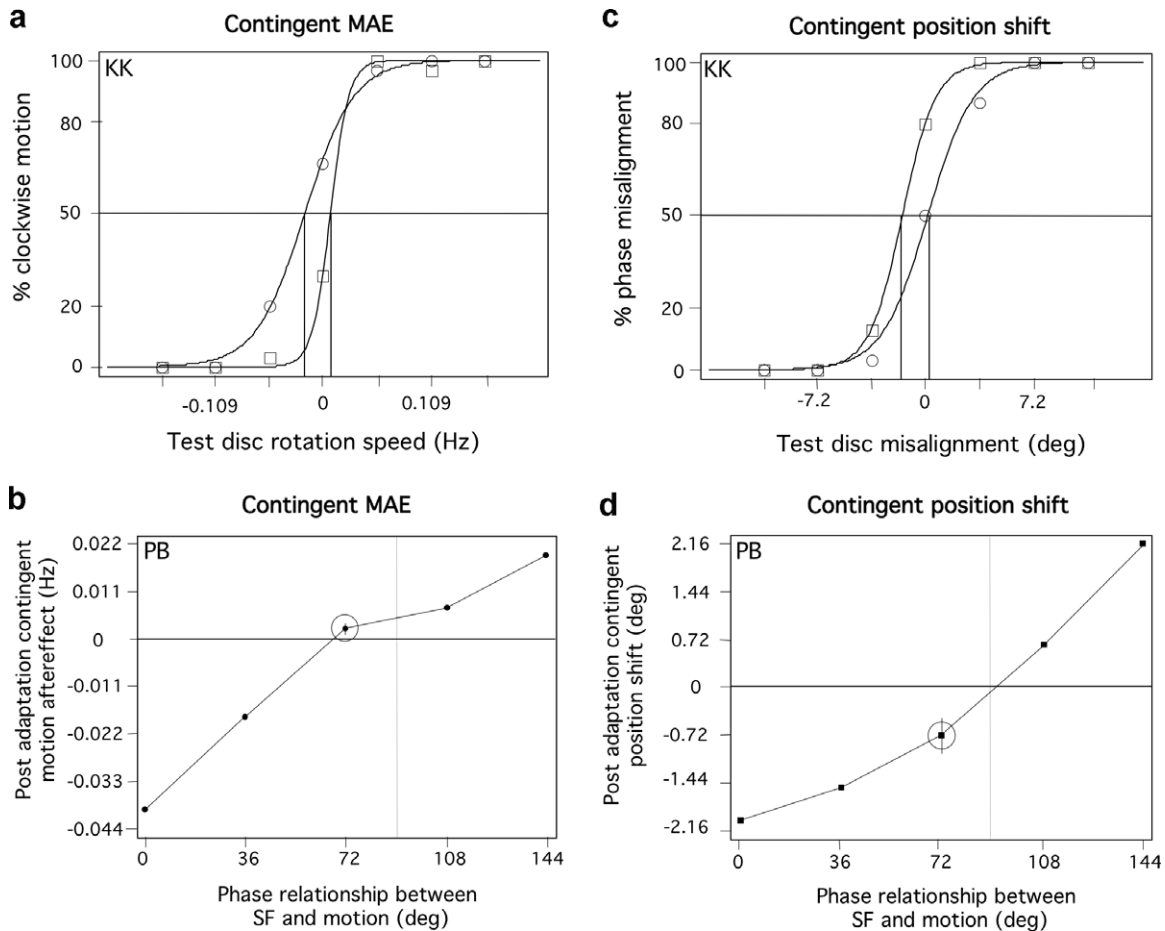
Fig. 2. Results for two representative subjects. Left panels show the spatial frequency-contingent MAE for one condition (72 deg phase offset between motion and spatial frequency), and right panels show the contingent position shift following the same motion adaptation. (a) The contingent MAE; representative psychometric functions for both high (squares) and low (circles) spatial frequency test patterns. The abscissa shows the physical rotation of the test grating, and the ordinate shows the frequency of subject responses that were in a clockwise direction. The point of subjective equality (PSE) is the 50% point on the psychometric function and reveals the physical rotation required to null the MAE. The difference between the PSEs for low and high spatial frequency is a measure of the magnitude of the contingent MAE. If there were no contingent aftereffect, there would be no difference in the PSEs for low and high spatial frequency test patterns. The difference between the two PSEs (high minus low spatial frequency, $X^2(1) = 11.2$, $P < 0.05$) in (a) is from the same condition as the circled data point plotted in (b). Each data point on the graph (b) is the difference between the PSEs for high and low spatial frequency test patterns; positive and negative values indicate the presence of a contingent MAE. The abscissa shows the phase offset between direction and spatial frequency changes during adaptation (as in Fig. 1d). Only 0–180 deg is shown, as the data for 180–360 deg were mirror symmetrical and therefore flipped and merged. (c) The contingent position shift experiment; representative psychometric functions for both high (squares) and low (circles) spatial frequency test patterns. The abscissa shows the physical phase shift in the test gratings, and the ordinate shows the frequency of subject responses that one grating was misaligned clockwise (as in Fig. 1c). The point of subjective equality (PSE) is the 50% point on the psychometric function and reveals the physical phase misalignment required to null the position shift. The difference between the PSEs for low and high spatial frequency ($X^2(1) = 11.5$, $P < 0.05$) is a measure of the magnitude of the contingent position shift. (d) Each data point on the graph is the difference between the PSEs for high and low spatial frequency test patterns. Comparing (b) and (d) reveals that, following exactly the same motion adaptation, the contingent MAE is in a direction opposite that of the contingent position shift. Error bars, 95% confidence intervals for 72 deg condition.

individual subject data reveals that this dissociation between perceived motion and position holds for each subject (Fig. 4). This indicates that nulling the contingent MAE and position shift required differential time-courses of motion and spatial frequency information at the time of adaptation. Any amplitude differences between the contingent MAE and position shift are irrelevant, as the test stimulus duration and measurement scale differ for each judgment, and scaling the data does not alter the position of the zero crossings or the opposing signs of the effects (at 72 deg phase offset). Likewise, an absolute difference in the magnitude of the MAE for high and low spatial frequency

patterns explains neither the difference in the zero crossings nor the opposing effects. Moreover, a global motion aftereffect that influences the relative positions of the test patterns as a whole is unlikely, as subjects reported them to appear aligned at all times.

Fig. 5 shows the results of the third experiment—the color-contingent MAE (a replication of Arnold et al., 2001), as well as the color-contingent position shift. Like Arnold et al. (2001), there was a lag in the zero crossing for the color-contingent MAE ($t_{(7)} = 2.33$, $P < 0.05$). This indicates that to null the color-contingent MAE, the color changes had to lag behind the direction reversals. Unlike spatial
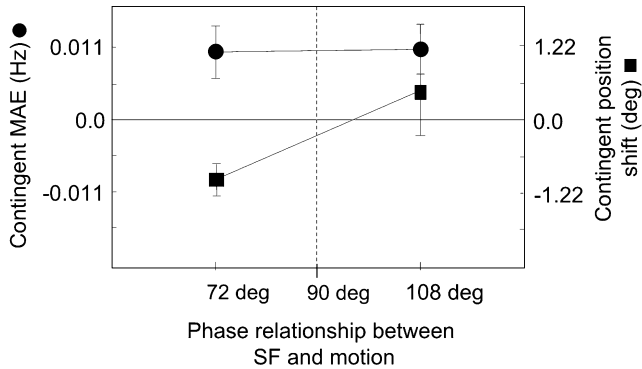
Fig. 3. Results for four subjects. The format of the graph is similar to that in Fig. 2b. The abscissa shows the phase relationship between direction and spatial frequency during adaptation; the two phase offsets of interest were 72 and 108 deg. The vertical dashed line indicates a 90 deg phase relationship, in which each direction of motion was paired for an equal duration with each spatial frequency during adaptation (Fig. 1d, bottom panel); it is at this 90 deg phase offset that no contingent aftereffect should be observed, if both spatial frequency and motion changes were synchronously processed. The spatial frequency-contingent MAE (left ordinate) was above zero (circles), indicating that the zero-crossing for the contingent MAE occurred well before 90 deg (consistent with Fig. 2). The spatial frequency-contingent position shift (right ordinate, squares), on the other hand, crosses zero at about 90 deg phase offset—precisely where one would expect there to be no contingent aftereffect. There was a significant interaction between the contingent MAE and position shifts as a function of the phase offset (Friedman test, $X^2(3) = 8.0$, $P < 0.05$). Most importantly, at 72 deg phase offset, the contingent position shift was significantly below zero ($t_{(3)} = -4.92$, $P = 0.008$). The MAE, on the other hand, was significantly above zero ($t_{(3)} = 2.7$, $P = 0.035$). Further, at 72 deg phase offset, there was a significant difference in the sign of the MAE and position shift effects (Mann–Whitney test, $Z = -2.31$, $P = 0.021$). Error bars, between subjects ±SEM.
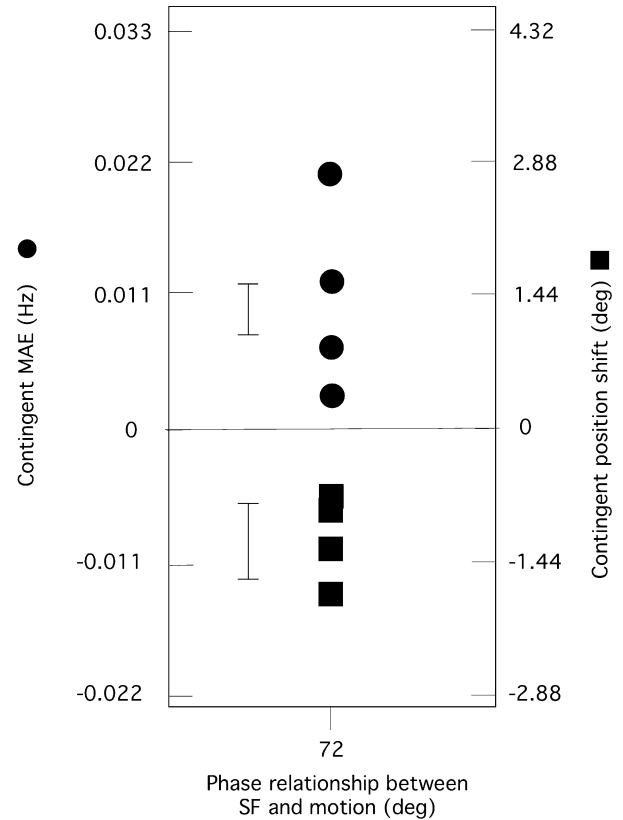

Fig. 4. Individual subject results showing contingent motion (circles) and position (squares) aftereffects following adaptation to a 72 deg phasic pairing between changes in spatial frequency and motion. The zero crossing represents the absence of a contingent MAE or contingent position shift. All subjects in this condition perceived the position of the test disc to be displaced in a direction opposite to that of the judged rotational direction. Error bars are representative within-subject ±95% confidence intervals.

frequency defined patterns (Fig. 3), there was not a significant difference between the time-courses of the color-contingent MAE and position shift ($t_{(3)} = 0.9$, $P > 0.05$). The results indicate that the relative time-course of visual feature processing depends on the particular features that are presented; the perceived motion and position of an object can be dissociated (Fig. 3) but are not always (Fig. 5).

4. Discussion

There were two main results of the experiments above. First, there was an asynchrony between spatial frequency changes relative to motion direction changes, and there was an asynchrony between color changes relative to motion direction changes. Second, and more importantly, the results revealed that these asynchronies hinged on the type of perceptual judgment being made—the differential asynchronies for different features (spatial frequency versus motion direction) *depended on* whether the perceived motion or position of the object was being judged.

The goal of the first two experiments was to measure whether a spatial frequency-contingent MAE could be temporally and spatially dissociated from a contingent position shift. If perceived motion and position are determined by a single neural population, and given absolutely identical

adapting stimuli as in the experiments above, there is no reason to expect that the time-course of the perceived MAE should differ from the perceived position shift. However, the results revealed a dissociation in both the time-course and spatial direction of the contingent MAE and position shift (Figs. 3 and 4). Therefore, there must be distinct populations of neurons that adapt on different time-courses and independently give rise to the perceived motion and position of the test stimuli. This does not imply that different populations of neurons *always* give rise to perceived motion and position of objects, or that perceived motion and position are *always* dissociated. Indeed, the color-contingent MAE and position shift revealed a case in which the motion and position of a test pattern were not dissociated (Fig. 5). The dissociation between the spatial frequency contingent MAE and position shift (Figs. 3 and 4), therefore, provides sufficient evidence that the coding of perceived motion and position *can* be dissociated.

The results presented here further demonstrate that binding between visual object attributes (i.e., spatial frequency and motion) are relative both with respect to each other, and also to the type of judgment being made. If visual attributes are synchronously bound throughout processing, then
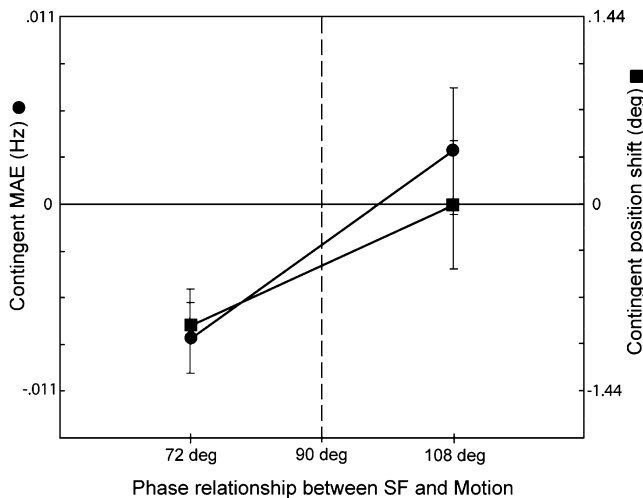
Fig. 5. Results for four subjects in the color-contingent MAE and position shift experiment. The format of the graph is identical to that in Fig. 3. The color-contingent MAE (left ordinate) was below zero (circles), indicating that the zero-crossing for the contingent position shift and MAE occurred after the 90 deg phasic pairing (replicating Arnold et al., 2001). The color-contingent position shift (right ordinate, squares) was also below the zero and was not significantly different than the MAE ($t_{(3)} = 0.9$, $P > 0.05$). A linear regression fit to the merged data revealed a ~33 ms asynchrony (lag in the zero crossing) which was significant ($t_{(7)} = 2.33$, $P < 0.05$). This effect is consistent with, though smaller than, the effect found by Arnold et al. (2001).

adaptation to a stimulus whose direction of motion is paired exactly half the time with each spatial frequency pattern should produce no contingent aftereffects. For judgments of object motion (the contingent MAE in Experiment 1), however, spatial frequency changes had to lead motion reversals to null the contingent MAE. This finding of differential temporal processing of spatial frequency and motion is analogous, but in a temporally opposite direction, to that found for object color and motion (Fig. 5; Arnold et al., 2001, 2003; Bedell et al., 2003; Clifford et al., 2003; Johnston & Nishida, 2001; Moutoussis & Zeki, 1997; Nishida & Johnston, 2002). Although this could be due to differential latencies for motion and spatial frequency (or motion and color), there are alternative possibilities. For example, spatial frequency and motion processing may involve different temporal profiles of activity (just as color and motion may too; Arnold & Clifford, 2002; Bedell et al., 2003; Clifford et al., 2003). This is distinct from the differential latency argument in that the visual system (the adapting neurons) may be sensitive to the profile of incoming activity over time, rather than discrete events such as reversals. This argument has been raised before to explain the asynchrony observed in the color-contingent MAE (Fig. 5; Arnold & Clifford, 2002; Bedell et al., 2003; Clifford et al., 2003; Johnston & Nishida, 2001; Nishida & Johnston, 2002). A similar explanation could hold for the spatial frequency-contingent MAE in Fig. 3. Nishida and Johnston (2002) proposed another possible explanation for the color-motion asynchrony, which may also apply to other sorts of visual information. According to these authors, temporal representations, or "time

markers," of stimulus attributes may be misaligned, resulting in false binding. In fact, any of these models could explain the color-motion or spatial frequency motion asynchrony reported in Fig. 3. Regardless of which model is correct, however, the results here demonstrate that the asynchrony between visual features depends on the type of perceptual judgment being made: the spatial frequency-contingent MAE can occur in one direction while the contingent position shift is in an opposite direction (i.e., an object can appear to drift in one direction while appearing shifted in the opposite direction; Figs. 3 and 4). Therefore, whichever model explains the color-motion asynchrony (or the spatial frequency-motion asynchrony) must take into account the fact that separable populations of neurons can code the motion and position of an object.

5. Conclusion

Taken together, the findings presented here suggest that there is a dynamic binding problem: that different attributes of individual objects are coded by distinct neural populations and can independently give rise to temporally dissociated percepts (such as the motion and position of a pattern). This may support the notion that distributed modular coding of visual features independently gives rise to awareness of different dimensions of a single object, thereby limiting the binding problem (Zeki, 2001).

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